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Mating Calls of Some Frogs From Thailand

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During a year's ecological study of amphibians and reptiles at the Sakaerat Experimental Station, located 250 km. N.E. of Bangkok, I had the opportunity to observe and record vocal activity of 22 species (11 genera and 4 families) of frogs. The mating calls of some of these species have been described in word form previously, but to my knowledge none has been analyzed from recordings.

Dr. Joe T. Marshall has also recorded mating calls of some Thai frogs. Those species recorded by him with which I have had no field experience are not included herein. His material is on deposit at the American Museum of Natural History.

METHODS AND MATERIALS

All calls were recorded on Scotch Brand No. 150-9 magnetic recording tape at 7½ i.p.s. using a Uher 4000 Report-L portable tape recorder. Analysis was by a Kay Electronics Sonagraph Model 6061B, using the 80-8000Hz frequency scale with narrow band filter (45 Hz) unless otherwise stipulated. The amplitude display unit was used to resolve temporal intensity patterns, particularly pulse repetition frequency and pulses per note. Playback was by a Crown Series 8000 tape recorder. The system, record to playback, is essentially flat ±3db over the frequency range of the analyzer.

Calling individuals were captured and preserved for positive identification in most cases; at least one calling specimen for each species was captured with the exception of *Kaloula pulchra*. The

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tapes and specimens are deposited at Field Museum of Natural History.

The terminology that has accumulated in association with call analyses is difficult to apply consistently to different types of frog calls. The following definitions are those used by current workers (Straughan, personal communication).

Since the darkness of the sonagraph trace is proportional to the source intensity, dominant frequency was taken as the darkest portion of the frequency traces on the sonagram. Where no discrete dominant was present, I took the entire frequency range of the darkest portion as the dominant. A fundamental frequency was recognized where a distinct frequency band lay between the dominant frequency and the baseline on the sonagram. Harmonic content is described when there is a regular pattern of frequency bands on the sonagram. A change of frequency within a note (fig. 14C) is called frequency modulation. Intensity modulation refers to a noticeable change in intensity within a note (fig. 5).

A call group consists of a series of repeated calls. A call consists of a series of repeated notes (fig. 9), a single note (fig. 3), or a series of pulses (fig. 7). A note may consist of a single pulse (no pulse), may be partially pulsed (fig. 3), or may consist of a series of pulses (fig. 2A).

Temperature is known to affect pulse rate. Unfortunately, temperatures were not recorded in every instance, but the records for which temperatures are available are presented in the species accounts.

ACKNOWLEDGMENTS

Noel Kobayashi, Prasert Lohavanijaya, Frank Nicholls, Sukhum Pongsapipatana, all of the Applied Scientific Research Corporation of Thailand, my wife Miriam and daughter Laura facilitated the fieldwork in Thailand, especially at Sakaerat. Jay M. Savage and Ian Straughan, University of Southern California, allowed me the use of the tape recorder and sonagraph. Dr. Straughan gave needed assistance with the sonagraph. Richard G. Zweifel, American Museum of Natural History, loaned Marshall's tapes and specimens for comparison. Robert F. Inger, Field Museum of Natural History, and Straughan carefully read the manuscript. Field work in Thailand was supported by National Science Foundation grant GB 7845X.

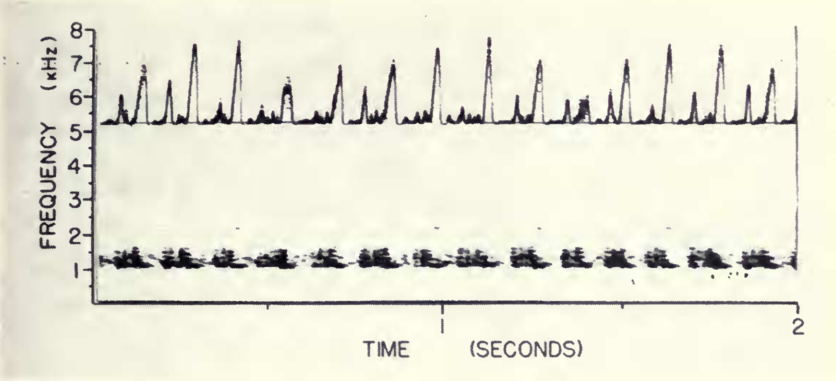

FIG. 1. The mating call of *Bufo melanostictus*, WRH 69-4, with amplitude display.

SPECIES ACCOUNTS

Bufonidae. Figure 1.

Eight calls from three specimens of *Bufo melanostictus* were analyzed (fig. 1). The calls are long trills of from 4–30 seconds. The pulse rate for a call recorded at an air temperature of 25°C is 13.2 pulses per second, counting all pulses. Maximum sound energy is spread over the frequency range 1000–1700 hz. The call does not have harmonics.

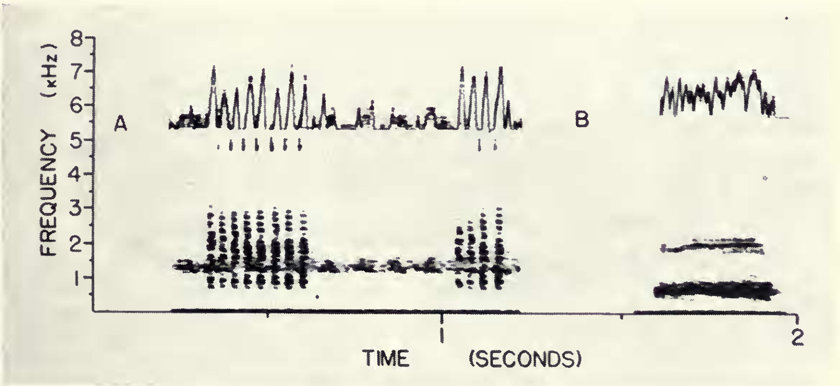

FIG. 2. A, The mating call of *Calluella guttulata*, WRH 69-3, with amplitude display. *Bufo melanostictus* in background. B, The mating call of *Glyphoglossus molossus*, WRH 69-1, with amplitude display.

Microhylidae. Table 1, Figures 2–9.

The call of *Calluella guttulata* (fig. 2A) consists of a series of pulsed notes lasting from .14–.37 seconds. Each note is composed of from 4–10 pulses; the pulse rate ranges from 27–33 per second. Maximum sound energy of the poorly tuned note is spread over the frequency range 700–3200 hz. There is no distinct fundamental frequency; poorly differentiated harmonics may or may not be present. Frequency and intensity modulations are absent.

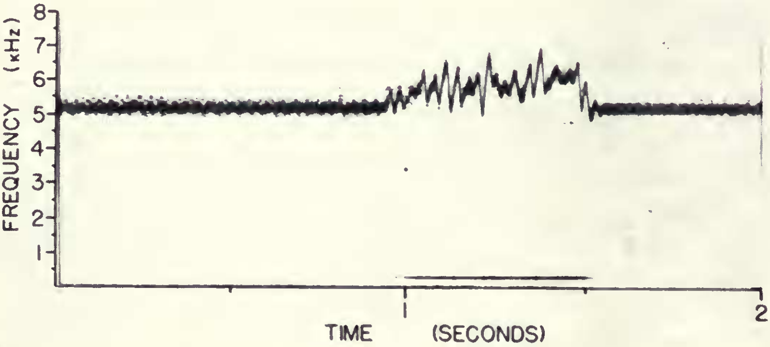

FIG. 3. The mating call of *Kaloula pulchra*, WRH 69-31, with amplitude display.

The call of *Glyphoglossus molossus* (fig. 2B) consists of a single partially pulsed note lasting from .30–.32 seconds. Each note is composed of from 12–19 pulses; the pulse rate ranges from 40–59 pulses per second. Maximum sound energy of the moderately well-tuned note is spread over the frequency range 300–1100 hz. The dominant frequency is the same as the fundamental. Two moderately differentiated harmonics are present at approximately 2000 and 3500 hz. The lower harmonic has the more energy. Intensity modulation is present.

The call of *Kaloula pulchra* (fig. 3) consists of a single partially pulsed note lasting .56–.60 seconds. Each note is composed of from 18–21 pulses; the pulse rate ranges from 32–35 pulses per second. The dominant frequency of the well tuned note is 250 hz. Well-defined harmonics are absent; the dominant frequency is equal to the fundamental. Frequency and intensity modulations are absent.

The call of *Microhyla berdmorei* (fig. 4) consists of a series of pulsed notes lasting .09–.26 seconds. Each note is composed of 3–9

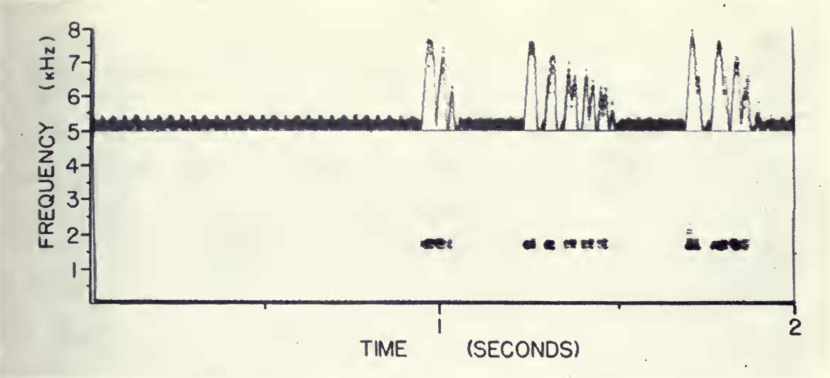

FIG. 4. The mating call of *Microhyla berdmorei*, WRH 69-39, with amplitude display.

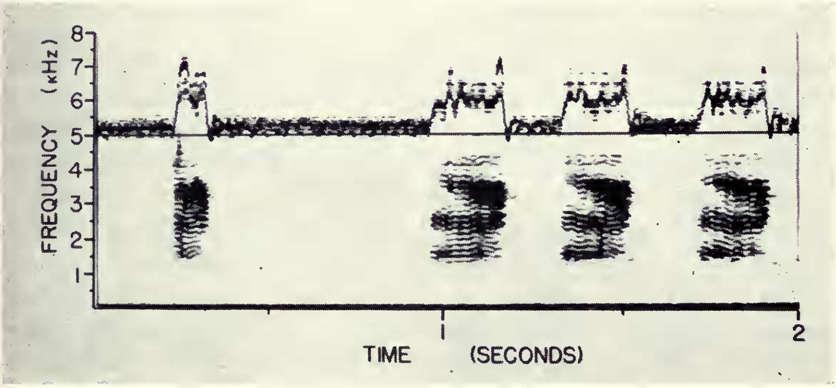

FIG. 5. The mating call of *Microhyla butleri*, WRH 69-11, with amplitude display.

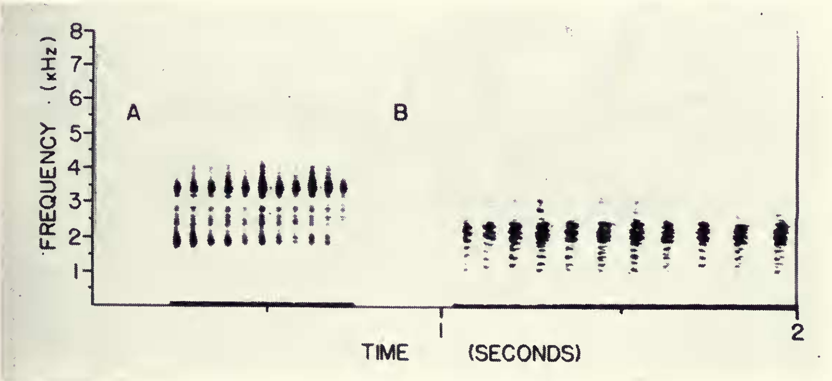

FIG. 6. A, The mating call of *Microhyla heymonsi*, WRH 69-9. B, The mating call of *Microhyla pulchra*, WRH 69-17.

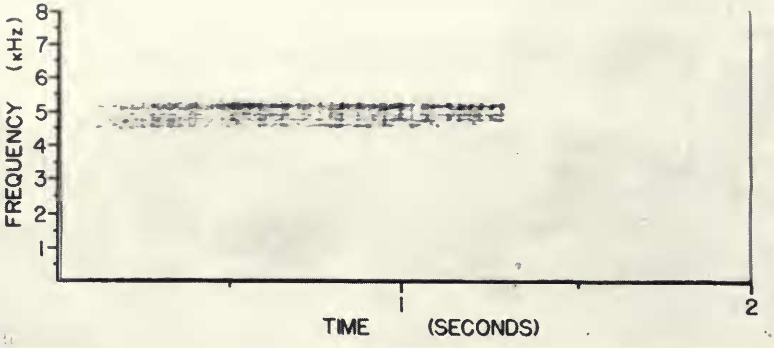

FIG. 7. The mating call of *Microhyla inornata*, WRH 69-19.

pulses; the pulse rate ranges from 33–35 per second. The dominant frequency of the moderately well-tuned note is spread over the 1500–1800 hz frequency range. Well-defined harmonics are absent; the fundamental frequency equals the dominant. Frequency and intensity modulations are absent.

The call of *Microhyla butleri* (fig. 5) consists of a series of partially pulsed notes, each note lasting .16–.21 seconds. Each note is composed of 6–7 pulses per note; the pulse rate ranges from 28–44 pulses per second. Maximum sound energy of the poorly tuned note is spread over the frequency range 1200–4500 hz. Harmonics are absent; the fundamental frequency equals the dominant. A

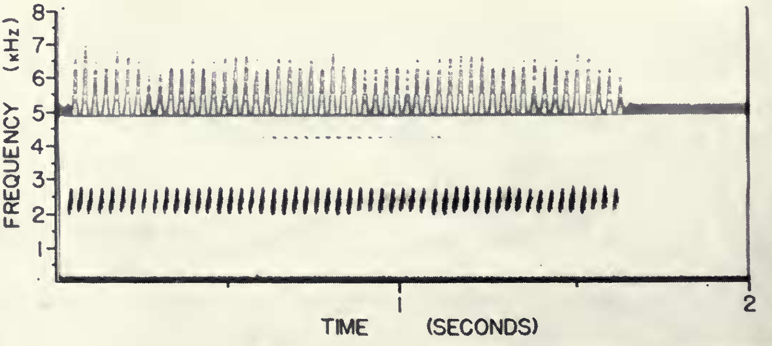

FIG. 8. The mating call of *Microhyla inornata*, WRH 69-19, played at half speed, analyzed with wide band filter, with amplitude display. The frequency scale is doubled and the time scale is half of the scales figured.

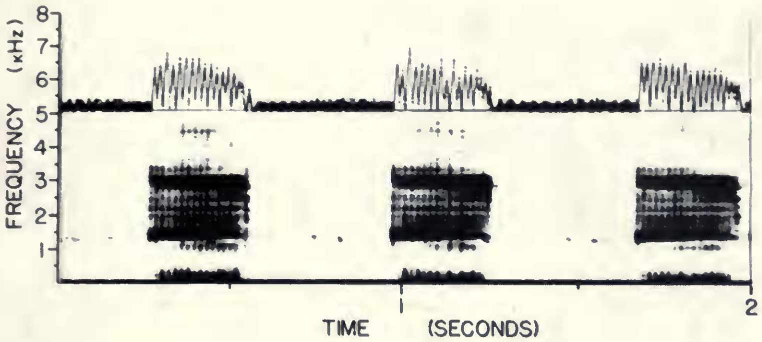

FIG. 9. The mating call of *Microhyla ornata*, WRH 69-2, with amplitude display.

strong intensity modulation is present, giving a distinctive, rising sound to the note when heard by the human ear.

The call of *Microhyla heymonsi* (fig. 6A) consists of a series of pulses, a call lasting .48 seconds. The single call analyzed had 11 pulses at a pulse rate of 23 pulses per second recorded at an air temperature of 28°C. Maximum sound energy of the poorly tuned call is spread over the frequency range 1700–3000 hz. Harmonics are absent; the fundamental frequency equals the dominant. The call lacks frequency and intensity modulation.

The call of *Microhyla inornata* (figs. 7, 8) consists of a series of pulses. The call lasts from .79–2.02 seconds. Each call is composed of 52–83 pulses; the pulse rate is approximately 66 pulses per second. Maximum sound energy of the poorly tuned call is spread over the frequency range 4400–6500 hz. Harmonics are absent; the fundamental frequency equals the dominant. The call lacks frequency and intensity modulation. The call sounds like a cricket rather than a frog.

The call of *Microhyla ornata* (fig. 9) consists of a series of notes, each note lasting .23–.31 seconds. Each note is composed of 10–18 pulses; the pulse rate ranges from 53–60 pulses per second recorded at air temperatures of 25–28°C. Maximum sound energy of the poorly tuned note is spread over the frequency range 1200–3500 hz. The fundamental frequency ranges from 80–500 hz. A poorly differentiated harmonic lies in the 4500–5000 hz frequency range. An intensity modulation is distinct in most of the tracings, giving a rising sound to the note when heard by the human ear.

TABLE 1.—Comparison of characteristics of mating calls of nine species of Microhylidae

N=Number of calls analyzed; parentheses enclose the number of specimens recorded

Species	N	Duration of calls or notes in seconds	Pulses/ call or note	Pulses/ second	Dominant frequency band in hz	Fundamental	Intensity Modulation	Harmonics
Calluella guttulata	4(1)	.14–.37	4–10	27–33	700–3200	absent	absent	absent or weak
Glyphoglossus molossus	6(1)	.30–.32	12–19	40–59	300–1100	absent	weak	present
Kaloula pulchra	2(1)	.56–.60	18–21	32–35	250	absent	absent	absent
Microhyla berdmorei	3(1)	.09–.26	3–9	33–35	1500–1800	absent	absent	absent
butleri	11(2)	.16–.21	6–7	28–44	1200–4500	absent	present	absent
heymonsi	1(1)	.48	11	23	1700–3000	absent	absent	present
inornata	4(2)	.79–2.02	52–83	66	4400–6500	absent	absent	absent
ornata	15(3)	.23–.31	10–18	53–60	1200–3500	absent	weak or present	present
pulchra	3(2)	1.42–1.92	10–20	7–10	1000–2500	absent	absent	absent

The call of *Microhyla pulchra* (fig. 6B) consists of a series of pulses. The call lasts 1.42–1.92 seconds. Each call is composed of 10–20 pulses; the pulse rate ranges from 7–10 per second recorded at an air temperature of 25°C. Maximum sound energy of the moderately poorly tuned call is spread over the frequency range 1000–2500 hz. Harmonics are absent; the fundamental frequency equals the dominant. The call lacks frequency and intensity modulation.

Each species call is quite distinct when heard in the field; these distinct differences are tabulated (Table 1).

Ranidae. Table 2, Figures 10–15

At the research site, the vast majority of *Ooeidozyga laevis* uttered two types of calls (A and C of Table 2 and fig. 10). Call type A consists of a single note lasting .03–.08 seconds. Each note consists of a single pulse. Maximum sound energy of the well-tuned call centers about two frequency ranges, 2000 hz and/or 3600 hz. The dominant frequency may be associated with the second and/or fourth harmonic frequencies. Three to seven harmonic frequencies are present at approximately 2000, 2800, 3600, 4200, 5000, and 5800 hz. The call lacks frequency and intensity modulation.

Call type C consists of a series of notes, each note lasting .03–.05 seconds. Each note is composed of a single pulse. The pulse rate ranges from 8–9 per second recorded at an air temperature of 30°C.

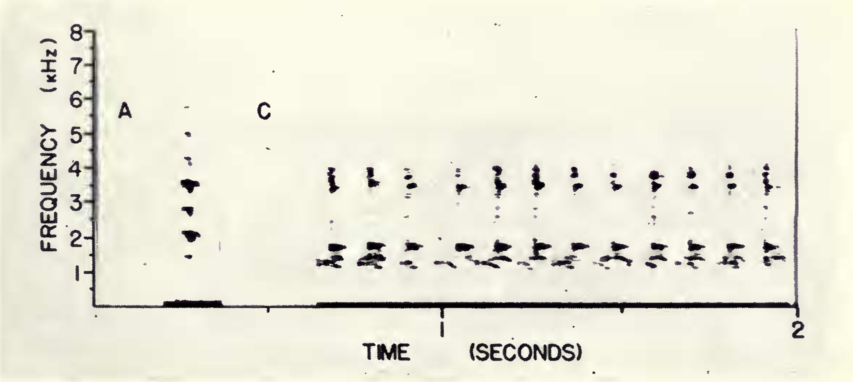

FIG. 10. Mating calls of *Ooeidozyga laevis*. A, Call type A, WRH 69-5. C, Call type C, WRH 69-13.

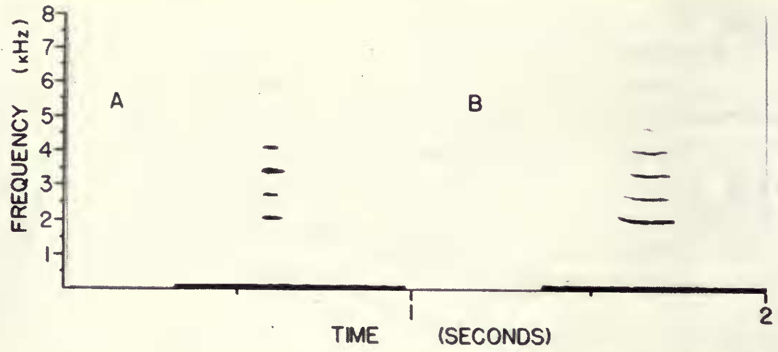

FIG. 11. Mating calls of *Ooeidozyga laevis* calling from the same pond. A, Call type A, WRH 69-16. B, Call type B, WRH 69-15.

Maximum sound energy of the moderately poorly tuned call is spread over the frequency range 1700–1900 hz. The dominant frequency is equal to the fundamental. A single rather indistinct harmonic is found in the 3500–4000 hz frequency range. A slight increasing or decreasing frequency modulation is found in the harmonic frequencies at the end of the call.

The call group consists of irregularly spaced call type A's ending with call type C.

Dr. Marshall recorded individuals of *Ooeidozyga* which had a different call. On April 3, 1969 I recorded both call types at the same locality (fig. 11). Our first reaction was that two sympatric species

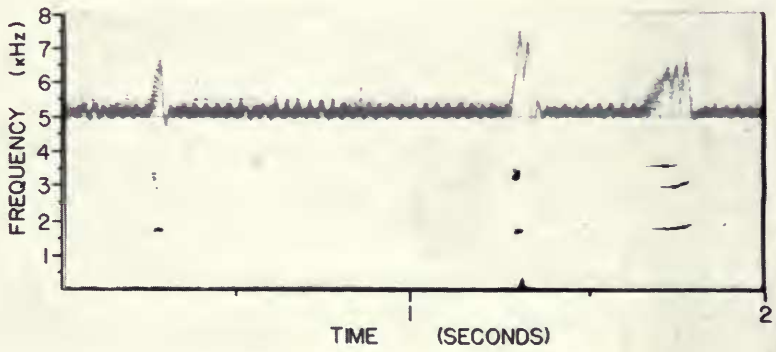

FIG. 12. Mating call of *Ooeidozyga laevis* illustrating call types A and B from a single individual, WRH 69-36, with amplitude display.

were involved. The unusual call, note type B (Table 2, fig. 11), was the only call heard from individuals of the "second" species. That is, the call of these individuals lacked the typical type C end of an *Ooeidozyga laevis* call group. Comparison of the sonagrams of call types A and B recorded in sympatry (fig. 11) indicate they differ basically only in note duration. Calling males of both call types were captured and proved morphologically indistinguishable. On August 2, 1969, I recorded one male *Ooeidozyga* that produced all three note types (types A and B only shown on fig. 12). This male was from the same pond at which recordings were made on April 3. I interpret the type A and B notes to be individual variation within a single species.

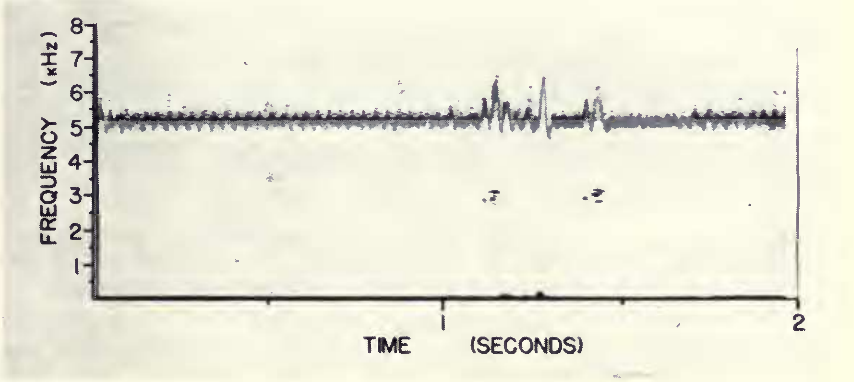

FIG. 13. The mating call of *Ooeidozyga lima*, WRH 69-34.

Ooeidozyga lima has two call types similar to *O. laevis;* a call group consisting of irregularly spaced single note calls ending with a call consisting of many rapid notes. I recorded only the first part of the call (Table 2, fig. 13). The call consists of a single note lasting .05–.06 seconds. Each note consists of two pulses. Maximum sound energy of the poorly tuned call is spread over the frequency range 2800–3200 hz. The call lacks harmonics; the fundamental frequency is equal to the dominant. The call lacks frequency and intensity modulation. The call of *O. lima* sounds very distinct from any of the call types of *O. laevis*.

The call of *Rana limnocharis* (fig. 14A) consists of a series of partially pulsed notes, each note lasting .11–.16 seconds. Each note is composed of 5–7 pulses. Maximum sound energy of the poorly tuned call is spread over the frequency range 2300–2800 hz.

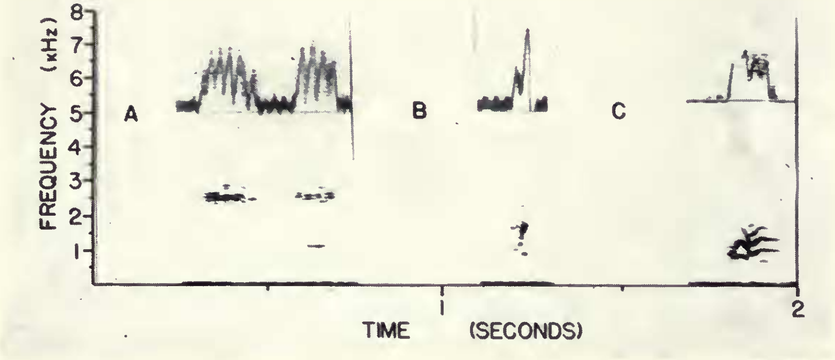

FIG. 14. **A,** The mating call of *Rana limnocharis*, no number, with amplitude display. **B,** The mating call of *Rana livida*, WRH 69-40 with amplitude display. **C,** The mating call of *Rana nigrovittata*, WRH 69-27, with amplitude display.

A fundamental frequency lies at approximately 1250 hz. No harmonics above the dominant are present. The call lacks frequency and intensity modulation.

The call of *Rana livida* (fig. 14B) consists of a partially pulsed note. The only note analyzed is composed of two pulses, the note lasts .04 seconds. The dominant frequency of the well-tuned call modulates from 900–1800 hz. A single harmonic modulates from 1500–2200 hz; the fundamental frequency equals the dominant.

The call of *Rana nigrovittata* (fig. 14C) consists of a partially pulsed note. The duration of the call ranges from .16–.21 seconds. Each note is composed of 3–4 pulses. The dominant frequency of the well-tuned note modulates in a complex manner (see fig. 14C) between 900 and 1500 hz. A fundamental frequency modulates between 500 and 1000 hz. Two to three harmonics above the dominant modulate between approximately 1200–1800, 1400–2000, and 1700–2000 hz respectively.

Rana pileata is the only species of *Rana* recorded that exhibited two call types. Call type A (fig. 15, first two tracings) sounds like a cross between WONK! and a stone dropping in water. The call consists of a pulsed note lasting .12–.14 seconds. Each note is composed of 2–4 pulses. Maximum sound energy of the poorly tuned call is spread over the frequency range 200–1000 hz. There are no harmonic frequencies; the fundamental frequency equals the dominant. A frequency modulation occurs between 500 and 1000 hz in one component of the tracing.

TABLE 2.—Comparison of characteristics of mating calls of six species of Ranidae. N=Number of calls analyzed; parentheses enclose the number of specimens recorded

Species	N	Duration of calls or notes in seconds	Pulses/ call or note	Dominant frequency band in hz	Fundamental	Frequency modulation	Harmonics	Note type
Ooeidozyga laevis	7(4)	.03–.08	1	1500–2200	absent or present	absent	present	A
laevis	3(2)	.15–.17	4	1800–2200	absent	present	present	B
laevis	3(2)	.03–.05	1–2	1700–1900	absent	absent or weak	present	C
lima	2(1)	.05–.06	2	2800–3200	absent	absent	absent	A
Rana limnocharis	4(2)	.11–.16	5–7	2300–2800	present	present	absent	
livida	1(1)	.04	2	900–1800	absent	present	present	
nigrovittata	2(2)	.16–.21	3–4	900–1500	absent or present	present	present	
pileata	3(1)	.12–.14	2–4	200–1000	absent	present	absent	A
pileata	3(1)	.11–.16	5–8	250–500	absent	weak	absent	B

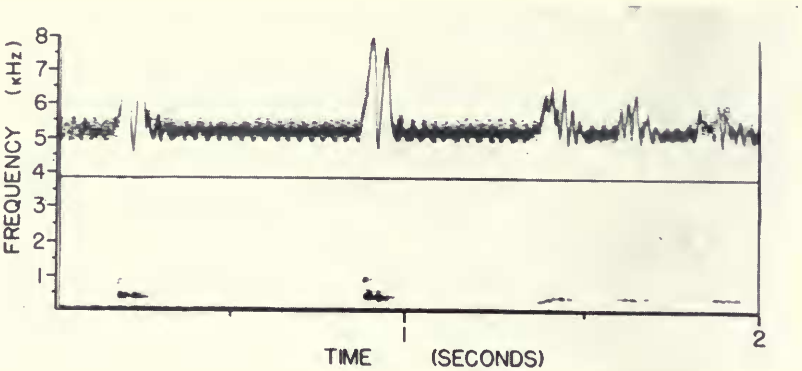

FIG. 15. The mating call of *Rana pileata* WRH 69-33, with amplitude display.

Call type B (fig. 15, last three tracings) sounds like snoring. The call consists of a series of pulsed and partially pulsed notes, each note lasting from .11–.16 seconds. Each note is composed of 5–8 pulses. The dominant frequency of the moderately well-tuned call lies between 250–500 hz. No harmonic frequencies are present. The notes of the call may have slight frequency modulations.

A call group of *Rana pileata* consists of call A given at spaced intervals; call B is given at intervals only when the frogs are most actively calling.

Rhacophoridae. Table 3, Figures 16–20

The call of *Chirixalus nongkhorensis* (fig. 16A) is composed of from 1–2 nonpulsed notes; i.e., each note consists of a single pulse. Each note lasts .02–.03 seconds. Maximum sound energy of the poorly tuned call is spread over the frequency range 3300–4000 hz. Harmonic frequencies are absent; the fundamental frequency equals the dominant. The call lacks both frequency and intensity modulation.

The call of *Chirixalus vittatus* (fig. 16B) consists of a series of from 1–4 nonpulsed notes, i.e., each note consists of a single pulse. Only one note was recorded and analyzed. The note lasted .05 seconds. Maximum sound energy of the moderately poorly tuned note is spread over the frequency range 1750–2000 hz. Harmonic frequencies are lacking; the fundamental frequency equals the dominant. The call lacks both frequency and intensity modulation. The first few times *Chirixalus vittatus* called, there was but one note

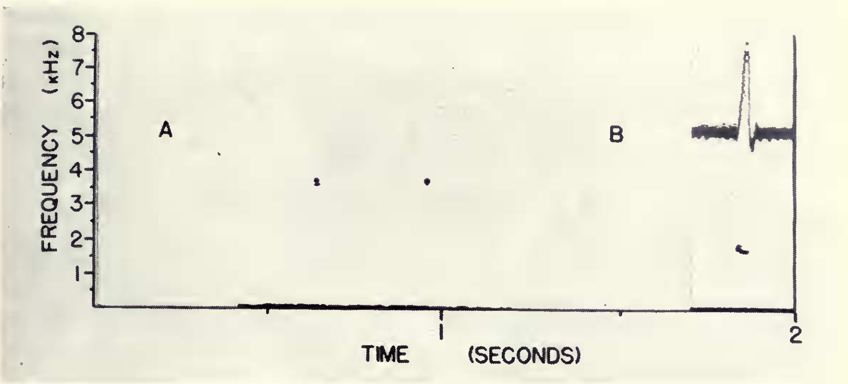

FIG. 16. A, The mating call of *Chirixalus nongkhorensis*, WRH 69-32. B, The mating call of *Chirixalus vittatus*, WRH 69-37, with amplitude display.

per call. Later in the season, the species commonly had up to four notes per call.

The call of *Philautus parvulus* (fig. 17) consists of a series of 1–7 nonpulsed notes, i.e., each note consists of a single pulse. Each note lasts from .02–.04 seconds. Maximum sound energy of the poorly tuned call is spread over the frequency range 2250–3250 hz. Harmonic frequencies are lacking; the fundamental frequency equals the dominant. The call lacks both frequency and intensity modulation. *Philautus parvulus* starts calling with one note per call, then increases by one note each succeeding call until the maximum number of notes per call is reached. *Chirixalus vittatus* and *Microhyla pulchra* also called in this manner, but not with the observed absolute

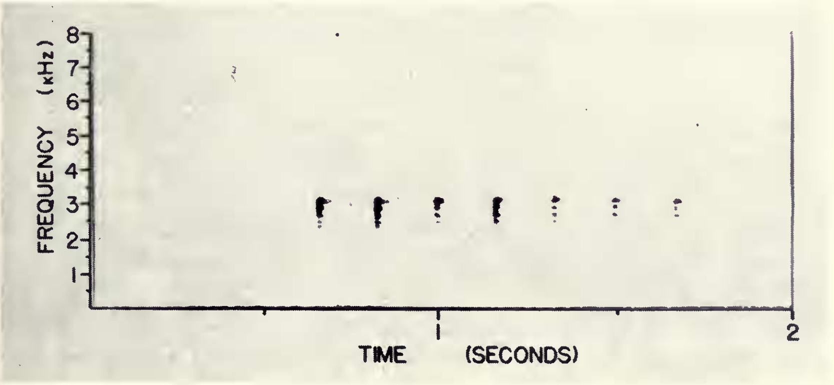

FIG. 17. The mating call of *Philautus parvulus*, WRH 69-30.

regularity of adding one note per call as observed in *Philautus parvulus.*

The call group of *Polypedates leucomystax* consists of two call types (fig. 18). Call type A (fig. 18A) consists of a pulsed note lasting .23–.38 seconds. Each note is composed of 4–5 pulses. Maximum sound energy of the poorly tuned call is spread over the frequency range 300–2600 hz. Harmonic frequencies are lacking; the fundamental frequency equals the dominant. The call lacks frequency modulation, but may have a slight increase in intensity at the end. Call type B (fig. 18B) consists of a pulsed note lasting from .12–.25 seconds. Each note is composed of 2–4 pulses. Maximum sound energy of the poorly tuned call is spread over the frequency range 1700–3100 hz. Harmonic frequencies are lacking; the fundamental frequency equals the dominant. The call lacks both frequency and intensity modulation. There did not appear to be any pattern of how the call types were organized into a call group.

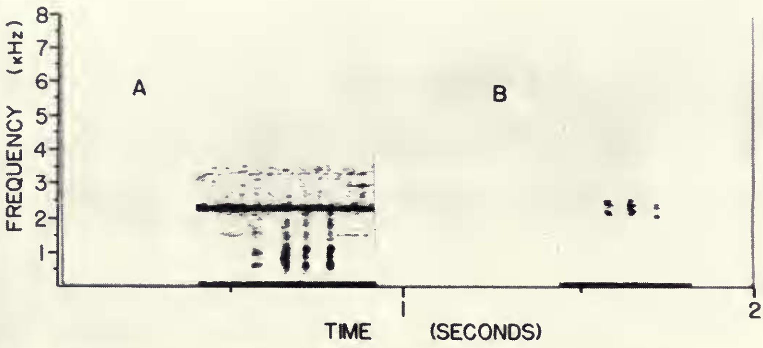

FIG. 18. Mating calls of *Polypedates leucomystax*. A, Call type A, WRH 69-14. B, Call type B, WRH 69-23.

The call group of *Rhacophorus appendiculatus* is composed of two call types (fig. 19). Call type A (fig. 19A) consists of a single note. The only note analyzed is composed of a single pulse lasting .04 seconds. Maximum sound energy of the moderately well-tuned note lies between 2500–2600 hz. Harmonic frequencies are lacking. The fundamental frequency appears to equal the dominant. The call lacks both frequency and intensity modulation. Call type B (fig. 19B) consists of a pulsed note. The only note analyzed is composed of seven pulses, lasting .48 seconds. Maximum sound energy of the

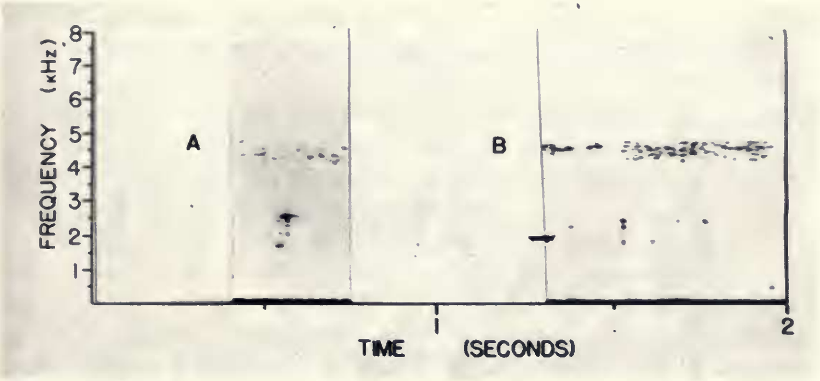

FIG. 19. Mating calls of *Rhacophorus appendiculatus*. A, Call type A, WRH 69-26. B, Call type B, WRH 69-26.

poorly tuned call is spread over the frequency range 1600–2500 hz. The recording and subsequent sonagram are of too poor a quality to determine if a distinct fundamental frequency is present or frequency or intensity modulations are present. A call group started with type A given at various intervals, ended with a series of call type B calls.

The call group of *Rhacophorus bimaculatus* is composed of two call types (fig. 20). Call type A (fig. 20A) consists of a single pulsed note lasting .04–.09 seconds. Maximum sound energy of the poorly tuned call is spread over the frequency range 1900–2800 hz. Harmonic frequencies are lacking; the fundamental frequency equals the dominant. The call lacks both frequency and intensity modulation. Call type B (fig. 20B) consists of one or two pulsed notes, each lasting

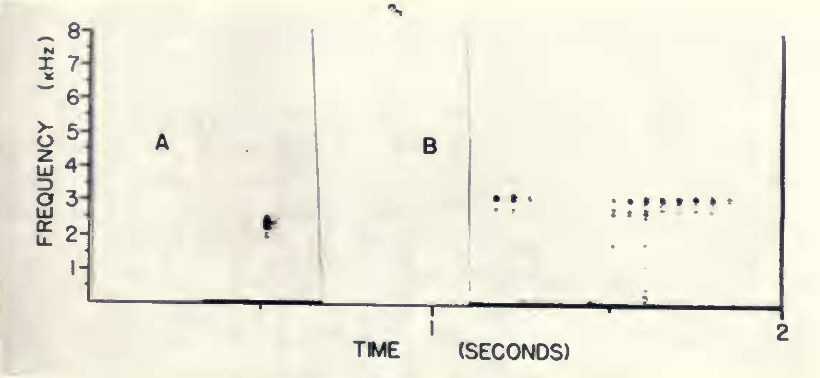

FIG. 20. Mating calls of *Rhacophorus bimaculatus*. A, Call type A, WRH 69-22. B, Call type B, WRH 69-35.

TABLE 3.—Comparison of characteristics of mating calls of six species of Rhacophoridae
N=Number of calls analyzed; parentheses enclose the number of specimens recorded

Species	N	Duration of calls or notes in seconds	Pulses/ note	Dominant frequency band in hz	Fundamental	Note type
Chirixalus nongkhorensis	2(2)	.02–.03	1	3300–4000	absent	
vittatus	1(1)	.05	1	1750–2000	absent	
Philautus parvulus	3(1)	.02–.04	1	2250–3250	absent	
Polypedates leucomystax	3(2)	.23–.38	4–5	300–2600	absent	A
leucomystax	3(3)	.12–.25	2–4	1700–3100	absent	B
Rhacophorus appendiculatus	1(1)	.04	1	2500–2600	absent	A
appendiculatus	1(1)	.48	7	1600–2500	absent	B
bimaculatus	4(2)	.04–.09	1	1900–2800	absent or weak	A
bimaculatus	2(1)	.10–.34	3–8	1800–3300	weak	B

.10–.34 seconds. Each note is composed of 3–8 pulses. Maximum sound intensity of the poorly tuned call is spread over the frequency range 1800–3300 hz. The recordings and subsequent sonagrams are of poor quality, but it appears that a weak fundamental frequency is spread over 80–500 hz, and that no pronounced frequency or intensity modulations are present. Call group composition is identical to that of *Rhacophorus appendiculatus.*

The calls of *Chirixalus nongkhorensis* and *vittatus* sound similar to the human ear as do those of *Rhacophorus appendiculatus* and *bimaculatus. Chirixalus nongkhorensis* and *vittatus* occur in sympatry at the research site; with practice I was able to discriminate the calls of the two species at a given pond. As shown on Table 3, there is a difference in frequencies. *Rhacophorus appendiculatus* and *bimaculatus* were never taken in sympatry. The recordings of each of these two species are of poor quality and do not allow for detailed comparisons between the species.

DISCUSSION

The usefulness of mating calls in determining relationships is well established, particularly when two morphologically similar species exhibit divergent call types. The usefulness of mating calls in determining relationships above the species level is not as well documented. The data presented herein demonstrate that mating calls can aid in determining higher relationships, but the method has limitations.

One way of approaching the data is to look at the calls of the members of genera and families for common uniting characteristics. An extension of this approach is to look for a call prototype from which all calls of the group may be derived. The microhylid and rhacophorid calls analyzed appear as though the calls of each of the families could have been derived from a single call prototype. The prototype for the microhylid call would be composed of several pulses per note over a rather broad frequency range. If this prototype is assumed, the call has been channeled in many directions through selection. In some cases, the frequency response has become narrowed as in *Kaloula pulchra,* or broadened as in *Microhyla butleri;* the pulses have been jammed together as in *Microhyla inornata* or spread apart as in *Microhyla pulchra.* As shown in Table 1, the frequencies between 250 and 6500 hz have been partitioned among the species. Certain species, as *Microhyla butleri* and *M. ornata,* have been able to modulate the intensity of the call.

The rhacophorid prototype would consist of a component with a wide frequency range, lacking harmonics. The calls of *Chirixalus* and *Philautus* recorded are similar in having a single type of call which may consist of from one to several notes. Each of the species of *Polypedates* and *Rhacophorus* recorded has two call types. In *Polypedates* both call types are composed of several pulses per note, whereas the species of *Rhacophorus* have one call type that has a single pulse. In all forms with two call types, the difference between call types within a call group of a given species are in the number of pulses and frequency range.

Another way of organizing the data is to sort the calls by what appear to be different methods of sound production; in other words, sorting for fundamental types of calls. The calls reported appear to fit into three fundamental types: 1) Bufonidae, 2) *Rana* (Ranidae), and 3) Microhylidae, Rhacophoridae, and *Ooeidozyga* (Ranidae). If these groupings do indicate different mechanisms of sound production, two conclusions may be made. In some instances, calls may be useful in differentiating groupings, such as *Ooeidozyga* from *Rana*, and bufonids from the other families. In other instances, mating call production may give no indication of relationships, such as indicated by members of three families sharing common sound reproduction mechanisms (type 3 call). This, in turn, may indicate that methods of sound production are limited in frogs.

Mating calls may correlate with phenomena other than those associated with relationships. Konishi (1970) indicates two contradicting evolutionary pressures involving the physical properties of sound: 1) lower frequencies carry farther than higher frequencies, yet 2) "higher frequencies and wider frequency ranges . . . are more suitable for localization by binaural comparisons of intensity or time differences . . ." (p. 68). In more complex habitats, it would appear logical to assume that the exact location of the calling male by the female would be the most important factor; that is, frog calls in complex habitats would be predicted to have higher frequencies than those in simple habitats. To test this hypothesis, the data were organized in the following way. For the period of February 23, 1969 through December 31, 1969 records were kept on calling activity at ponds in four different ecological settings: 1) a pond next to a highway in an open situation; 2) three small ponds resulting from pits dug for road fill in a deciduous dipterocarp forest; 3) a series of ponds resulting from a small spring in partially cleared dry evergreen forest;

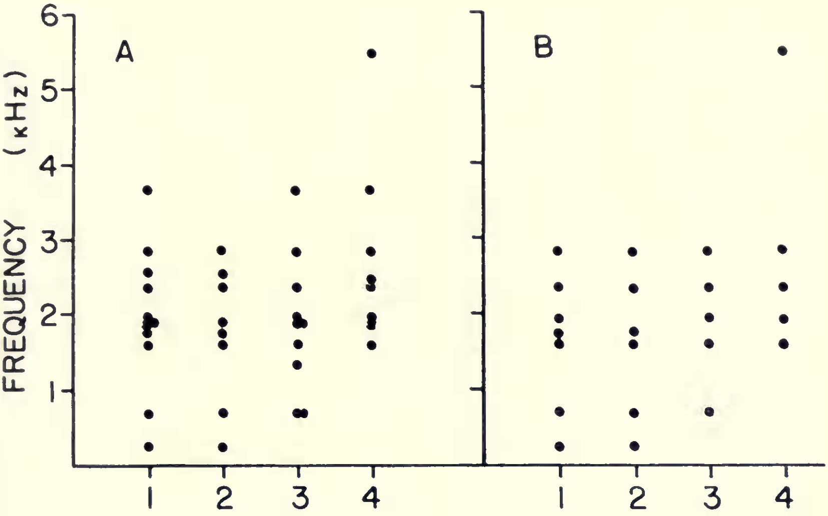

FIG. 21. Average frequency of dominant of each species in four vegetation types. Vegetation type 1 is the most open, type 4 the densest. A, All species. B, Microhylids only.

and 4) a naturally occurring temporary pond in the dry evergreen forest. From 1 to 4 represents a grade of increasing complexity and density of the vegetation. Results of calling activity by species were pooled for the year for each pond situation. An average dominant frequency was determined for each species by taking the average of the ranges reported. In the cases where a frog call contained two or more note types an average value of all the averages of the different note types was used. The frequency values were then plotted by ecological situation (fig. 21). There does appear to be a trend of higher dominant frequencies associated with denser vegetation (fig. 21A). It is obvious, however, that this trend is accounted for solely by members of the family Microhylidae (fig. 21B).

The chorus structure of members of the Microhylidae give further insight into the ecological meaning of physical parameters of sound coding systems. Male *Glyphoglossus* and *Kaloula* call while floating in the water of just-filled rain pools. Both are large species, locally abundant while calling, and at Sakaerat were found in the more open habitats. The two species have the lowest dominant frequencies of the microhylids recorded. The males can attract females over long distances; the females need only to locate the ponds, not individual males. All other species of microhylids analyzed call from the banks or from vegetation on the water surface and are smaller species.

The call of *Microhyla berdmorei* is characterized by a narrow frequency range of the dominant and a lower maximum dominant frequency than any of the other species of *Calluella* or *Microhyla* analyzed. Males were calling from isolated pools next to a flowing river (a habitat of rapid sound attenuation) and were the only species calling from such a habitat. Around each suitable pool, numerous males were calling. Apparently, the critical factor is similar to the situation as observed in *Glyphoglossus* and *Kaloula;* attracting females to a suitable microhabitat rather than to an individual male. The remaining species are characterized by calling males dispersed around a suitable pond situation. Here the apparent critical factor is the point location of the calling male by the female. The calls of this group of species are higher and have wider frequency ranges, satisfying the physical requirements for more accurate binaural point location of the sound source (Konishi, 1970).

Using the microhylids as an example, mating calls give the following information with respect to relationships. The calls of members of the family show a unity at the family level (remember the small sample size, however!). At the other extreme, the calls are most useful in distinguishing the species. The call data aid in distinguishing certain categories, but yield no information on the phylogenies of the categories involved. The correlation of call characteristics with habitat differences and types of mating call chorus indicate that other factors besides those associated with relationships are involved in the evolution of mating calls.

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